THE MOVEMENTS OF GREGARINES.

BY HOWARD CRAWLEY.

For the proper comprehension of the movements displayed by gregarines, it is advisable first to consider the form and anatomy of the animals. In a species like *Porospora gigantea* Van Beneden the ratio of length to breadth is 50–1, whereas *Lophocephalus insignis* Aimé Schn. is nearly spherical. It is obvious that the first of these two species can display movements of contortion which the second cannot. These are extreme cases, but gregarines may roughly be divided into long, slender and short, stout species, and in a discussion of their movements it is well to keep in mind the limitations to flexibility imposed on the latter merely on account of their shape.

Further limitations are imposed by the anatomical structure. From without inward, a polycystid gregarine displays epicyte, sarcocyte, myocyte and entocyte. The epicyte is a cuticular layer, the function of which is protective. It is always present, and varies considerably in thickness in the different species. The sarcocyte is a layer of clear protoplasm which, in a typical case, is continuous over the entire animal. This condition exists in such genera as *Gregarina*, *Stenophora* and *Amphoroides*. Frequently, however, the sarcocyte is lacking, except for the septum, which it constitutes, and in the immediately adjacent parts. These two layers may collectively be termed the ectosarc.

The myocyte is described by some authors as a part of the ectosarc; by others as a part of the endosarc (entocyte). It is made up of a layer of fibrils. Of these, the more conspicuous encircle the animal in a slightly spiral direction. The circular fibres are joined together by longitudinal and diagonal connectives, the whole system forming a net.

The entocyte of gregarines is probably much like that of other protozoa. It is composed of soft, distinctly alveolar protoplasm, liberally provided with the so-called granules of reserve.

It will be seen from the above that the ectosarc of gregarines may vary greatly in thickness. We may have a species in which both the component layers are thick. On the other hand, the epicyte may be thin and the sarcocyte absent. We probably have here an explanation for the difference in the rigidity of gregarines. Some species, such as

Stenophora julipusilli Leidy, tend to maintain a certain definite shape. Changes of this shape may be extensive, but are usually of short duration. Further, the contortions are of such a character that the true form is by no means disguised, and the resumption of this true form is always a very sudden process. We may conclude from this that the ectosarc is stiff and elastic. Under the force of the contractile elements it may suffer contortion, but as soon as the force is released the proper form is resumed with a sudden jerk. The comparison may be made with a hollow india-rubber ball, or, perhaps better, it may be said that these gregarines behave as if their ectosarc were composed of india-rubber. They may further be compared with such ciliates as *Paramœcium,* at least in so far as regards the sudden resumption of the normal contour after a deformation.

On the other hand, gregarines like *Trichorhynchus pulcher* Aimé Schn. are highly polymorphic. Different individuals present quite different outlines, and these outlines are subject to continual and extensive changes. Their movements may not inaptly be termed amœboid. All polycystid gregarines possess what may be designated as a typical outline, but it is often difficult, in these polymorphic species, to determine what this typical outline may be. Their ectosarc, while extremely flexible and extensible, does not appear to possess any elasticity. In consequence, deformation may be carried to such an extent as to render the typical form wholly unrecognizable, nor is there ever seen that sudden resumption of the typical form so often displayed by such species as *Stenophora julipusilli.*

This difference appears to be due mainly to the sarcocyte. Usually, in these polymorphic animals, the ectosarc consists of epicyte alone. Further, the epicyte may be thin. The facts, then, are in accord with what we should expect on mechanical principles. The elastic species possess a sarcocyte; the polymorphic do not. It may therefore be inferred that the elasticity is due to the sarcocyte, and confirmatory evidence is furnished by the Monocystidea. These animals, which are frequently highly polymorphic, appear generally to lack a sarcocyte. The rule, however, is not absolute, since *Stenophora* (*Cnemidospora*) *spiroboli* Crawley, the protomerite of which is very flexible, possesses a thick sarcocyte.

Obviously, the ability of a gregarine to display changes of form depends upon two factors.[1] These are the flexibility of its ectosarc and the power of the contractile elements. It has been shown that

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[1] There is possibly a third factor, as will be pointed out below.

great differences exist in the first of these in different gregarines. I shall now consider the contractile element.

This is evidently the myocyte. The evidence that the myocyte is contractile is purely inferential, but none the less satisfactory. The fibre is the form always taken by differentiated contractile substance. Other protozoa, ciliates and flagellates, show like elements, and most of the movements displayed by polycystid gregarines are comprehensible only by assuming the myocyte to be a contractile system. On the other hand, certain movements exhibited by the polymorphic species cannot so readily be explained in this way, as I shall presently show.

Confining our attention for the moment to these movements for which the myocyte seems an adequate cause, they are found to be displayed by all gregarines. They are, however, as we should expect, far more definite in the elastic than in the polymorphic species. The most usual are mere bendings of the longitudinal axis, the character and extent of which appear to depend largely upon the shape of the gregarine and the nature of its ectosarc. The least extensive are bendings of the protomerite, which may take place in any plane. These may be so slight as to be difficult to detect, or so extensive that the axis of the protomerite comes to form a right angle with that of the deutomerite. They readily lead to a distortion wherein the angle in the longitudinal axis is formed in the deutomerite instead of at the septum. This may be a right angle even in such relatively thick species as *Stenophora julipusilli* Leidy. In *Gregarina dicœli* Crawley, which is a vermiform gregarine with a thin epicyte and no sarcocyte, this distortion becomes more evident. The protomerite and anterior part of the deutomerite bend round to form a hook, the anterior surface of the protomerite being directed backward. As the point in the longitudinal axis where the original bending takes place moves further and further backward, the hook becomes larger and larger until the gregarine forms a U. This U may pass into a circle and the circle into a coil or a spiral. *Gregarina polydesmivirginiensis* Leidy[2] displays contortions of exactly the same character. Animals such as *S. julipusilli* Leidy frequently bend double, but the circular or coiled condition cannot well be assumed by any but the long slender gregarines.

When only the protomerite is involved, the movement is frequently first to one side and then to the other. This may also happen when the anterior part of the deutomerite participates along with the proto-

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[2] According to Léger et Duboscq (1903), this species belongs to the genus *Stenophora*, since it stands very close to the *Stenophora nematoides* of these authors.

merite. Occasionally, also, it is the posterior part of the deutomerite which is bent, the balance of the animal maintaining its original position. Yet however varied these bendings may be, they are all of them only contortions whereby the longitudinal axis loses its original straightness.

Their cause is contractions of the myocyte. It is easy to see how such contortions could be produced by a shortening of the longitudinal fibres of one side, possibly aided by a contraction of the transverse fibres at the place where the bendings originate. This pull on the part of the myocyte is resisted by the ectosarc to a greater or less extent, contingent upon its rigidity and elasticity. This is shown by the suddenness with which the ectosarc springs back to its original position, which presumably takes place when the pull exerted by the myocyte ceases to act. The behavior of the ectosarc in such a case is, as previously stated, precisely what it would be were it composed of india-rubber.

The following point is also worthy of note. When a gregarine begins to curve, one side is lengthened and the other shortened. The ectosarc is evidently capable of a certain amount of contraction, since a crescentic form may be assumed with the shortened side still presenting a smooth contour. But if the bending be carried to any considerable extent, the inner surface folds, the number and depth of these folds depending upon the shape of the gregarine and the extent of the curvature. This shows that the power of the ectosarc to contract is limited.

A movement of the same general character as the bending is one whereby the longitudinal axis is shortened. It consists in the pulling of the protomerite into the deutomerite, as one may withdraw the hand into the sleeve. I have noticed this in a number of species, although it is by no means so frequently seen as the bending. It is displayed indifferently by animals which are progressing and those which are not. As in the case of the bending, the return to the typical shape, in the elastic species, is by a sudden jerk. This movement is explainable by a shortening of the longitudinal fibres around a given zone of the animal's body.

There is finally the so-called peristalsis. This, as defined by Delage et Hérouard (1896), consists of "Contractions péristaltiques, produites par un étranglement transversal qui se propage le long du corps." It does not, however, admit of quite so simple a definition. It may be a swelling instead of a constriction. Further, it frequently happens that instead of a series of such constrictions or swellings there will be but one, which passes from the region of the septum to the posterior end of the animal. In the typical associations, as in *Gregarina*, this movement is described as passing from the anterior end of the primite to the posterior end of the satellite without the slightest pause. We have here a demonstration that it is not due to endoplasmic movements.

In general, the conspicuousness of the peristaltic movement depends on the character of the ectosarc. In the stiff, elastic forms this movement is by no means common, and when it does occur it generally consists of a single contraction. On the other hand, it is well displayed by the polymorphic species with thin ectosarcs. In one species, *Actinocephalus harpali* Crawley, I have frequently observed a disposition to rumple the edges of the body, so that they present a series of scallops. These scallops were seen to undergo slow changes in size and sometimes they moved slowly backward. I take this to be a peristaltic movement, although much slower than is usual.

The cause throughout is probably contractions of the circular fibres. Further, following the division which I have made, the peristaltic movement comes under the head of shortenings of the longitudinal axis.

The above are all the movements involving change of shape which can with absolute certainty be credited to contractions of the myocyte. They result in varied and frequently considerable alterations of the contour of the animal, but they can all be placed in two categories:

(1) Bendings and curvings of the longitudinal axis.
(2) Shortenings of the longitudinal axis.

The two may, and doubtless frequently do, take place at once, but apparently the first is by far the more frequent expression of the contractility of the myocyte.

There now remain for consideration a series of phenomena displayed by the polymorphic forms wherein the Polycystidea approximate the conditions normal to the Monocystidea. Of the several species which I have observed, they are best illustrated by *Trichorhynchus pulcher* Aimé Schn. This animal changes shape as readily as *Euglena* or even *Amœba*. The anterior margin of the protomerite may present a straight edge, a curve or a long tongue-shaped protrusion. The posterior end of the deutomerite may be bluntly rounded, sharply pointed or even bifurcated. The animal may also be so contorted as to lose all semblance to a polycystid gregarine and to present the kind of outline we associate with *Amœba*. These changes take place constantly, and by no means slowly, but always gradually. *Stenophora spiroboli* Crawley, another polymorphic species, has to be watched very patiently before the true form can be made out. It constantly displays contortions which are most conspicuous at the anterior end, and these contortions are of such a character that it is wholly impossible to say whether a given point of the surface is protomerite or deutomerite. From this end, moreover, little lobopodia were seen to arise and disappear.

In the case of a small gregarine from *Lithobius*, a very noteworthy movement was seen. This expressed itself as a slight peristalsis, the wave being evident at times on only one side. It was accompanied by a flow, *en masse*, of the granules of the entocyte. This flow, starting at the posterior part of the deutomerite, would pass forward until it struck the septum. Here the granular mass was deflected backward, the peristalsis being reversed at the same instant. In one case the nucleus was carried forward and backward along with the granules. This movement was seen both in animals that were progressing and those which were not. It was displayed constantly, but was generally very much faster when the animal was progressing. In one observation made, however, the gregarine showing this movement had its progression suddenly checked by striking an obstruction, and here the flow and peristalsis continued with unabated vigor. Frequently when gregarines are pinched by passing through narrow places, or when they bend, the entocyte is seen to flow. But in no other case amongst the Polycystidea which has ever come under my notice was the flowing anything like so free and extensive. These gregarines were very favorable for a study of the movements of the entocyte, since the number of granules was remarkably few and their flowing easy to observe.

A somewhat similar peristaltic movement was once seen in *Trichorhynchus pulcher* Aimé Schn. Here, the gregarine lying in one place, the wave arose at the posterior end and passed forward. The movements on both sides were not synchronous. It differed from the case just described in that there was no reversal, the movement being continuously forward.

The protrusion of the long tongue-shaped process by *T. pulcher* and of the lobopodia by *S. spiroboli* are not satisfactorily credited to activity of the myocyte. Such an action would appear to involve the spontaneous lengthening of relaxed fibres, which is scarcely possible. But even if it did not, the form of the myocyte, which is that of a fine-meshed net, would not seem to lend itself to such movements. They would necessitate an enormous elongation of a very small part of the system, and would thus predicate a complexity of action which we could hardly expect in so simple an apparatus. Without, however, desiring to prejudice the decision, it is advisable to see if an explanation may not be had along different lines.

The formation of pseudopodia in rhizopods is due to movements of the endosarc, and in gregarines the endosarc is evidently mobile. It may therefore be suggested that the polymorphism of certain of the Polycystidea is caused in the same way as it is in Rhizopoda. An endoplasmic flow, if by chance it were directed radially, would evidently result in such protrusions as are actually seen in *Trichorhynchus*. For it is to be remembered that such forms have a thin, extensible ectosarc, which would offer little resistance to such a flow. The difficulty in arriving at a decision is that the endosarc of most polycystids is so opaque that flowing movements might take place without it being possible to detect them. As I have already stated, the little gregarine of Lithobius is the only species at all favorable for a study of this element which has yet come under my notice.

In the Monocystidea, however, the conditions are more favorable. Flowing of the endosarc is a matter of common observation, and it has generally been taken to be the cause of their polymorphism. While this may be so, my own observations on monocystids lead me to question it. These were made on a species of *Diplocystis*, a parasite of *Allolobophora longa*. This gregarine has the form of a serpent. In the cases observed movements were constant. There would appear at any point of the body a swelling which passed rapidly either forward or backward. The endoplasm fills this swollen part, flowing into it in front and out of it behind. Two such swellings may arise simultaneously and, advancing toward each other, amalgamate. The large swelling thus produced would maintain a fixed size for a moment, and then from its central part two streams would start in opposite directions, and the swelling would rapidly disappear. In one case the peripheral granules in a swelling moved along with it, while those in the centre moved in the opposite direction.

An individual of this species was observed to burst, permitting the escape of a portion of the granular contents. The ectosarc thereupon contracted, and showed very plainly a series of striæ, parallel and spirally disposed. Evidently these striæ were the expression of a powerful myocyte.

Contractions of the myocyte would produce a flowing of the endoplasm; flowing of the endoplasm would result in extensions of the limiting layer. Hence, on purely *à priori* grounds, the one explanation has as much claim to consideration as the other. In the case of the phenomena just described, however, it seems far more reasonable to credit them to muscular action. They were movements evidently to be compared with the peristalsis of the Polycystidea, which, as I have pointed out, cannot be credited to endoplasmic currents. Moreover, they were so rapid and so evidently powerful that a comparison with what we see in *Amœba* fails. Further, if they were caused by endoplasmic movements, the myocyte is left without a function, which is a most improbable supposition.

It therefore seems more probable that the polymorphism of the Monocystidea is due to muscular action. Hence, by analogy, the polymorphism of the Polycystidea should be accounted for in the same way. Nevertheless, as I have indicated, this view has certain objections and the decision is better postponed until additional data are obtained.

In an article on the progression of gregarines (Crawley, 1902), I endeavored to show that when the protomerite of a gregarine is bent to one side or the other, the surface of the deutomerite shows a wave which passes backward and transversely at the same time. My observations also indicated that the extent of the bending of the protomerite conditioned the extent of this wave. Further, when the bending of the protomerite was first to one side and then to the other, that is, when it oscillated, the transverse component of the wave on the surface of the deutomerite was also first to one side and then to the other. I therefore regard these two manifestations of activity as due to the same contraction of the myocyte. That is, a contraction which causes the protomerite to bend causes also this wave to pass over the surface of the deutomerite.

Certain criticisms which have been made upon this paper lead me to suppose that I did not bring out this point as clearly as desirable. I shall therefore make use of a comparison. If we bare the forearm and then slowly close the fingers tightly, a muscular wave passes upward and outward along the dorsal surface of the arm. By alternately contracting and relaxing the fingers, this wave exhibits an alternate transverse movement. In this case, the conspicuous result of muscular contraction is the closing or opening of the hand, but it is necessarily correlated with the disturbance on the surface of the forearm. In the gregarine, the oscillation of the protomerite is the conspicuous manifestation of muscular activity, and, under ordinary conditions of observation, the only one which is seen. But it is always accompanied by the wave on the surface of the deutomerite. The result is that a given point on the gregarine's surface pushes backward and transversely upon whatever may be in contact with it. This brings about a movement of the entire animal in an opposite direction. The movement will be rectilinear or zigzag, dependent on the less or greater extent of the transverse movement. This last, in its turn, depends on the extent of the oscillation of the protomerite. Hence, when the gregarine is advancing in a straight line, the evidence for muscular action is very slight.

My observations also indicated that gregarines are sticky, and that they do not seem able to progress unless in contact with a surface. I was therefore led to postulate the stickiness as more or less of a necessity in progression, its *rôle* being to prevent slipping of the particular part in contact with either the slide or cover-glass. Later observations, however, have led me to modify this opinion. Contact appears necessary, but not necessarily contact with a continuous surface. The observations were as follows:

The host intestine was teazed on a cover-glass, under a limited quantity of salt solution. The cover-glass was then inverted, and supported on a ring. In this way a mount having considerable depth was obtained. The results were to show that gregarines are able to progress away from a surface provided they can get into contact with some solid matter. One, originally moving on the surface film on the bottom of the drop, pushed its way upward through the particles of host intestine. In such cases, however, progression is slow and apparently difficult, and accompanied by constant and violent contortions. It may, moreover, be stated that in proportion as the environment renders progression more difficult, the evidences for muscular activity become more obvious. Thus, when an advancing gregarine encounters a mass of loose host tissue, it frequently endeavors to bore or wriggle its way through, and muscular contractions at once become very extensive.

The ability of gregarines to make their way amidst particles of solid in a hanging drop suggests that, in some cases at least, progression is effected in somewhat the same way as that of a snail. The presence of an adhesive substance on the surface may assist, but the primary factor is the alterations of the contour of the surface. These are doubtless by no means so regular as those of the foot of a snail, nor is gregarine progression usually so smooth. Yet, without going into tedious details, it is easy enough to see how such movements could produce progression. When, however, progression is being effected on a smooth surface, the adhesive substance probably plays a part.

A curious phenomenon was once exhibited by a little gregarine of *Scolopocryptops sexspinosus*. This is a very active species, progressing continually in straight lines and curves of long radius. It would occasionally give a sudden jerk, and advance by perhaps its own length by a leap. This ability to leap was never seen in any other species.

There finally remains for consideration what is probably a form of the progressive movement. Prior to encystment gregarines pair, the association in a genus like *Gregarina* being apparently only precocious pairing. It may be "head to tail" as in *Gregarina*, or "head to head" as in *Pterocephalus*. In either case the pair bends double at its middle point, thus bringing the gregarines side by side. Before or during this last process the system begins to rotate. During the course of this rotation the two individuals become more and more closely apposed until a spherical form is assumed. Meanwhile a common covering is secreted, the cyst formed and eventually the rotatory movement ceases.

This movement is generally mentioned by those authors who have made observations on the encystment of gregarines, but no attempt appears to have been made to account for it. Bütschli (1881), however, states that muscular contractions are to be observed at the time when the two animals begin to fuse. The explanation advanced by Schewiakoff, that gregarines progress by means of the extension of a stalk of gelatinous fibres, is here manifestly inapplicable. Further, since according to the accounts the rotation continues until after a certain amount of a gelatinous investment is secreted, changes of surface contour would not seem to be of effect. One point, however, is worthy of attention. The rotation, both in nature and when the gregarines are on the slide, doubtless takes place when the animals are suspended in a liquid. The only opposition which the rotation encounters is then the friction of this liquid, and this would be almost infinitesimal. That is, it does not seem necessary to assume that the impulse lasts as long as the rotation itself. The latter, once started, would continue of its own momentum for probably a considerable period of time.

Accurate observations are, nevertheless, a desideratum, and, as I have stated, these are yet to be made. I have, however, at times observed a rotation on the part of solitary gregarines. One case was particularly striking. The gregarines, specimens of *Trichorhynchus pulcher* Aimé Schn., holding the body bent, moved around the circumference of a circle. The curved longitudinal axis of the animals formed an arc of this circumference, the radius of which was perhaps one-half the animal's length. That part of the circumference not occupied by the gregarine was filled with a mass of sundry small particles, the movements of which followed that of the gregarine. That is, there was evidently present a ring-shaped mass of invisible jelly which was continuous from the anterior to the posterior end of the gregarine. In this case, although the conditions for observation were favorable, no cause for the motion could be detected. I have also seen individuals of *Stenophora julipusilli* exhibit this rotation.

These phenomena, while not in any way explaining the cause of the rotatory motion, show that it is not necessarily correlated with encystment. It is merely one of the several phases of the mobility of gregarines, ordinarily most conspicuously in evidence at the time of encystment. It has been the custom to separate these several phases and to treat them as wholly distinct phenomena. This custom I believe to be unfortunate. It appears to me that all the motor phenomena which the Polycystidea display may be directly credited to contractions of the myocyte, with the possible exception of the amœboid movements of certain species, and the rotation. For these observational evidence is required before pronouncing a final decision.

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